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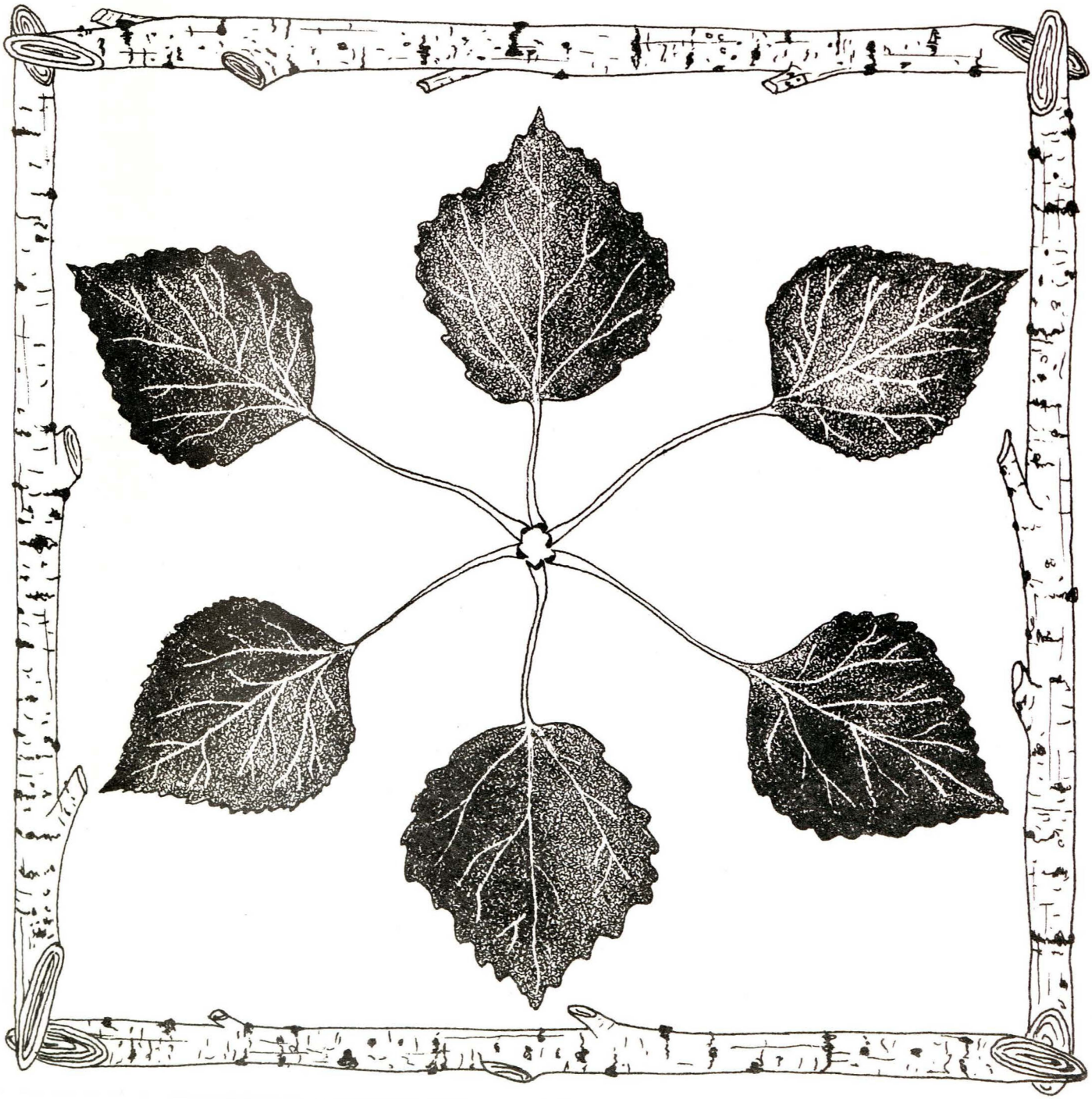
Research Paper
NC-321

Stockability, Growth, and Yield of the Circumboreal Aspens (*Populus tremuloides* Michx., *P. tremula* L.)

D. A. Perala, R. A. Leary, and C. J. Cieszewski



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1992 Folwell Avenue
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Manuscript approved for publication January 10, 1995
1995

Stockability, Growth, and Yield of the Circumboreal Aspens (*Populus tremuloides* Michx., *P. tremula* L.)

D.A. Perala, R.A. Leary, and C.J. Cieszewski

We show elsewhere (Perala *et al.*, in review) that quaking aspen (*Populus tremuloides* Michx.) and its Eurasian counterpart, *P. tremula* L., form a single circumpolar superspecies when viewed from the standpoint of self-thinning rates and stockability. Here we expand our examination to the d.b.h.-age relationships and to growth series measurements from permanent plots of aspen stands of varying densities reported in the literature. We also attempt to account for the curvilinear trend in the self-thinning relationship we detected in young stands that forced us in our first analysis to truncate our usable data set to older stands. The resulting equations satisfy the need for a framework to study variation in aspen stockability. The equations can give useful regional estimates as well, but will need refitting to local data to satisfy needs for finer resolution.

SPACING INDICES REVIEWED

The several spacing indices offered in the literature are essentially the same (Curtis 1970, Bredenkamp and Burkhart 1990). The index receiving the most attention recently, the self-thinning rule, is simply

[1] $W = k_0 * N^{-1.5}$

where

W = mean weight
N = stand density
k_0 = rate parameter

If we let W be proportional to D^2*H (Clutter *et al.* 1983), where

H = mean stand height,
D = quadratic mean d.b.h.,

and let H be proportional to D^0.8 (Curtis 1970), [1] becomes the limiting relationship,

[2] $D = k_1 * N^{-0.54}$.

That is,

[3] W::D^2*H::D^2.8::N^-1.5

becomes

[4] $D = k_1 * N^{(-1.5/2.8)} = k_1 * N^{-0.54}$

after introducing a rate parameter. The reciprocal relationship of [4],

[5] $N = (D/k_1)^{(1/-.54)} = (D/k_1)^{-1.85} = (1/k_1)^{-1.85} * D^{-1.85} = k_2 * D^{-1.85}$

is slightly more nonlinear (power of -1.85 vs. -1.6) than noted by Reineke (1933).

The k_1-parameters in these relationships were thought to be species-dependent, but not site- or age-dependent (Reineke 1933, Yoda *et al.* 1963, Drew and Flewelling 1977). Weller (1990) and Lonsdale (1990), however, offer evidence that the growing environment, as well as plant genetics, can alter both the rate and power parameters. The power, -3/2, should be considered a generality that is seldom achieved.

Variation among stands of a species in biomass packing has been termed "carrying capacity" (Strub and Bredenkamp 1985, Harrison and Daniels 1988), "average mass density" (Verwijst

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1989), and "stockability" (Debell *et al.* 1989). We will use the latter term.

A stand might be considered a packing space for a limited mass of water-conducting xylem (determined by an upper leaf area limit). The dead non-conducting heartwood provides only mechanical support but determines, in turn, how much crown can be supported by the stem (Dean and Long 1986). Therefore, the size-density limiting (self-thinning) relationship can be applied as mean d.b.h., height, weight, or volume dependency on stand density. But not all these relationships are independent of site and age. For example, consider two different sites with stands of the same age, mean d.b.h., and stocking density. The stand growing on the better site has taller trees and therefore greater mass than the other stand. On a traditional Reineke diagram, both stands would be represented by a single point; but on Czarnowski's and Yoda's diagrams, the stands would be represented by two points depicting different competition levels and likely different survival (Czarnowski 1961, Yoda *et al.* 1963). The better site with taller trees would be more tightly packed. Furthermore, given two more stands having the same height, d.b.h., and stocking density, but different ages (yet old enough to have attained maximum leaf area), the mass of these two stands would likely differ because tree taper usually decreases with age. These stands would be represented by single points on Reineke's and Czarnowski's diagrams, but again by two points on Yoda's. The site with older trees would be packed more efficiently. The density relation we use determines whether the stands appear different in competitive status and mortality rates. Because the Yoda relationship seems the most complete, it is reasonable to conclude that the Reineke relationship can benefit by extension of the factors, site and age.

Self-thinning relationships have their critics (Weller 1987; Zeide 1987, 1991; Lonsdale 1990), and have stirred lively debate (Osawa and Sugita 1989; Weller 1990, 1991); nevertheless, no useful alternative has been offered. Indeed, Zeide (1991) states "the self-thinning law is perfectly correct and even trivial within the assumptions explicitly stated by its authors *viz.* constant crown form and horizontal canopy closure.

Self-thinning relationships perform best when applied strictly to fully occupied sites (Osawa and Sugita 1989). Indeed, the relationship has been found useful in modeling productivity of several forest types, including *Pinus radiata* D. Don (Drew and Flewelling 1977), *P. contorta* Dougl. (Flewelling and Drew 1985), *P. resinosa* (Smith 1986, Smith and Brand 1988), *Pseudotsuga menziesii* (Mirb.) Franco (Drew and Flewelling 1979, O'Hara and Oliver 1988), *Alnus rubra* Bong. (Smith 1986, Hibbs 1987), *Thuja plicata* Donn. (Smith 1989), and *Eucalyptus grandis* (Hill) Maiden (Bredenkamp and Burkhart 1990).

METHODS

McFadden and Oliver (1988) integrated three two-dimensional stand models—tree size/tree number, tree size/stand age, and tree number/stand age—into a single compatible three-dimensional stand growth conceptual model. Self-thinning stands in their model might follow any one of three tree size/tree number dynamic trajectories, depending on initial stand density and age. In **trajectory I**, all stands follow the same trajectory at the same age; in **trajectory II**, stands follow the same trajectory but at different ages; and in **trajectory III**, stands of different ages or with different initial tree numbers follow different trajectories. We infer that site quality adds another dimension to stand growth (by affecting the rate of stand change) and to maximum density as well depending on stand history.

Weller (1990) distinguished two discrete approaches to modeling based on definition of the self-thinning line: (a) the **dynamic thinning line** (the log-linear self-thinning trajectory tracked by individual crowded stands), and (b) the **species boundary line** (the upper boundary self-thinning line attained only in extreme cases). We developed generic equations for aspen growth and yield based on Weller's species boundary line concept applied to the McFadden and Oliver model, trajectory III.

Data Sources

Stand data

Data for modeling stand d.b.h. growth, tree survival, and yield of quaking aspen, Eurasian aspen, and their hybrids were extracted from the published literature along with some data previously unpublished or limited in distribution (table 1). Some data for largetooth aspen (*P.*

Table 1.—*Data sources by species and provenance*

Author	Number of cases			Variable and range		
	Yield	Dynamic	Tabular	Site index	Age	Mean d.b.h.
				m @ 50 y	*yr*	*cm*
			P. tremuloides			
Alaska						
Gregory and Haack 1965			37	11-23	20-100	2-21
Prairie Provinces						
Bella 1975	9			20	3-6	1-2
Bella and DeFranceschi 1980			33	16-24	6-40	1-11
Kirby *et al.* 1957			27	13-19	20-100	4-29
Pike 1953	4	3		17-18	35-55	8-16
Steneker 1969	10	21		19-21	14-30	4-15
Steneker 1974	29	51		16-21	11-44	3-23
Rocky Mountains						
Baker 1925			5	17	100-140	24-33
Bartos and Lester 1984	3			8-10	54-82	13-21
Crouch 1981	1			17	66	20
Jones and Trujillo 1975	6			12-20	22	4-5
Kemperman and Barnes 1976	2			9-15	100-105	23-28
Schier 1975	5			9-12	70-92	15-23
Schier and Smith 1979	1			18	67	21
Walters *et al.* 1982	3			13-19	60-70	21-28
Great Lakes						
Barnes 1969	3			12-19	16-36	4-13
Brown and Gevorkiantz 1934			27	12-24	20-80	3-36
Day 1958	7	3		18-24	10-25	3-11
Graham *et al.* 1963			16	14-26	25-50	8-30
Hubbard 1972	4	6		27	7-24	3-14
Noreen 1968	9	5		24	4-20	1-10
Perala 1974		7		21	2-10	1-4
Perala 1978	7	48		23-25	13-53	4-31
Perala 1979	2			23-24	4-8	1-3
Perala 1984	2			23-27	12	5
Perala data filed	6	19		24	15-39	5-17
Perala and Alban 1982	2			21-22	40-49	18-24
Perala and Laidly 1989		24		25-31	5-21	3-13
Plonski 1960			51	16-24	20-100	6-33
Schlaegel 1971, 1972		60		18-24	10-62	5-35
Schlaegel 1975	1			24	40	18
Schlaegel and Ringold 1971		8		26	37-47	17-24
Newfoundland						
Page 1972			8	17	20-90	5-22
			***P. tremula* and hybrid**			
Scandinavia						
Elfving 1986		4		34	9-32	7-25
Haugberg 1958	34	69				
Vuokila 1977	2	11		22-23	11-48	3-25
Russia						
Vincent *et al.* 1950			50	11-24	10-100	1-34
TOTAL *P. tremuloides, tremula*	152	339	254	8-34	2-168	1-43
			P. grandidentata			
Michigan						
Graham *et al.* 1963			19	14-26	25-60	9-27
Koerper and Richardson 1980	3			16-27	52-60	14-19

grandidentata Michx.) were used to validate the models. These data comprised three sets:

(a) Yield set—singular empirical observations of aspen yield reported for unmanaged fully stocked stands. These were usually controls or initial conditions prior to experimental treatment. This set was used to model the relationship of variables acting upon stocking and the self-thinning relationship. The resulting equation defined the terms and their parameter values needed to model the dynamic set.

(b) Dynamic set—singular or serial empirical observations of aspen growth for both experimentally treated and untreated stands. Thinning was the only treatment specified except that Perala and Laidly (1989) fertilized as well, and the aspen hybrids were planted (Elfving 1986). This set was used to model stand growth and survival.

(c) Tabular set—smoothed yield data based on many observations over a geographical area (*e.g.*, Brown and Gevorkiantz 1934, Plonski 1960). These are found in "normal" or "average" yield tables. This set was used to confirm and validate the model determined from the yield set. These tables were constructed in different ways (hand-fitted or statistically derived regressions) from data taken from subjectively chosen field plots. Largetooth aspen yield and tabular data are included in this set.

Minimum stand data needed were tree number (all trees taller than 1.37 m), quadratic mean d.b.h., total age (but not younger than attainment of maximum stand density, usually 2 years), and site index. If either tree number or d.b.h. was missing, it was derived from given basal area according to

[6] $D = (12732*B/N)^{0.5}$

where

D = quadratic mean d.b.h., cm
B = stand basal area, m^2*ha^{-1}
N = stand density, $stems*ha^{-1}$

If site index was missing or given in a base year other than 50, it was estimated from accompanying or local tabular or graphical values. If these were unavailable, site index was estimated from

[7] $S = H_d/\{1.48*[1-\exp(-0.0214*A)]^{0.9377}\}$

(Gevorkiantz 1956, Lundgren and Dolid 1970) where

S = site index, m at 50 yr
H_d = mean total height of dominants and codominants, m
A = total stand age, yr

Other data, such as sapwood area or leaf area, were much too sparse to be useful.

These data conformed generally to the d.b.h.-age and the self-thinning relationships (figs. 1,2).

Environment data

Because the data sets are so wide ranging, we expected that latitude, longitude, elevation, and other environmental variables might account for some regional variation. The edaphic environment was seldom described adequately, but climatic data were sometimes given or could be inferred from other sources, *viz.*

total annual solar radiation, MJ/m^2*y (Budyko 1982)

mean July air temperature, C (Hambidge 1941, Anon. 1984)

total annual precipitation, mm (Hambidge 1941, Anon. 1986)

annual runoff, mm (Geraghty *et al.* 1973, Pearse *et al.* 1985)

These are based on long-term averages, often 30 years. For tabular data, these values were estimated for the centroid of aspen distribution within the stated provenance.

Model Development

Standard linear regression procedures (Weisberg 1985) were followed in preliminary modeling to

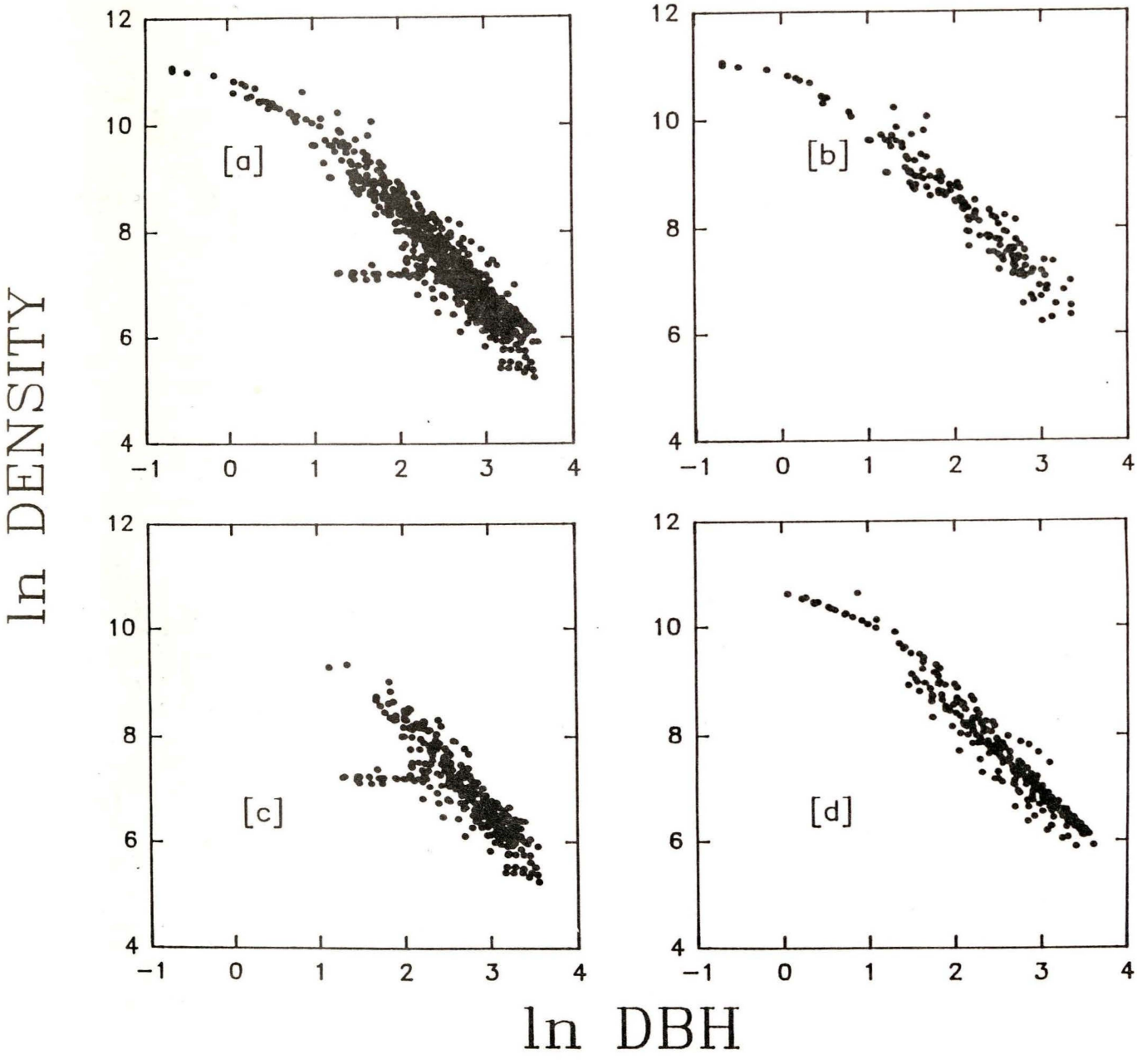

Figure 1.—*The relation of stand density to quadratic mean d.b.h. (double-logarithmic scale) for (a) the entire data set, (b) the yield set, (c) the dynamic set, and (d) the tabular set.*

identify significant variables. To linearize relationships and to stabilize variances, we transformed models to the logarithmic mode. Deviations about these models were routinely plotted over environmental variables, and screened for treatment, species, and lack-of-fit trends in scatter diagrams, box plots, and probability plots. Variables seemingly related to the deviations were introduced to the model, and new equations were solved. Variables were retained only if $p<0.01$. Nonlinear procedures (Wilkinson 1988) were used to develop the final equations that are expressed along with their statistics and interpretation in the original arithmetic mode.

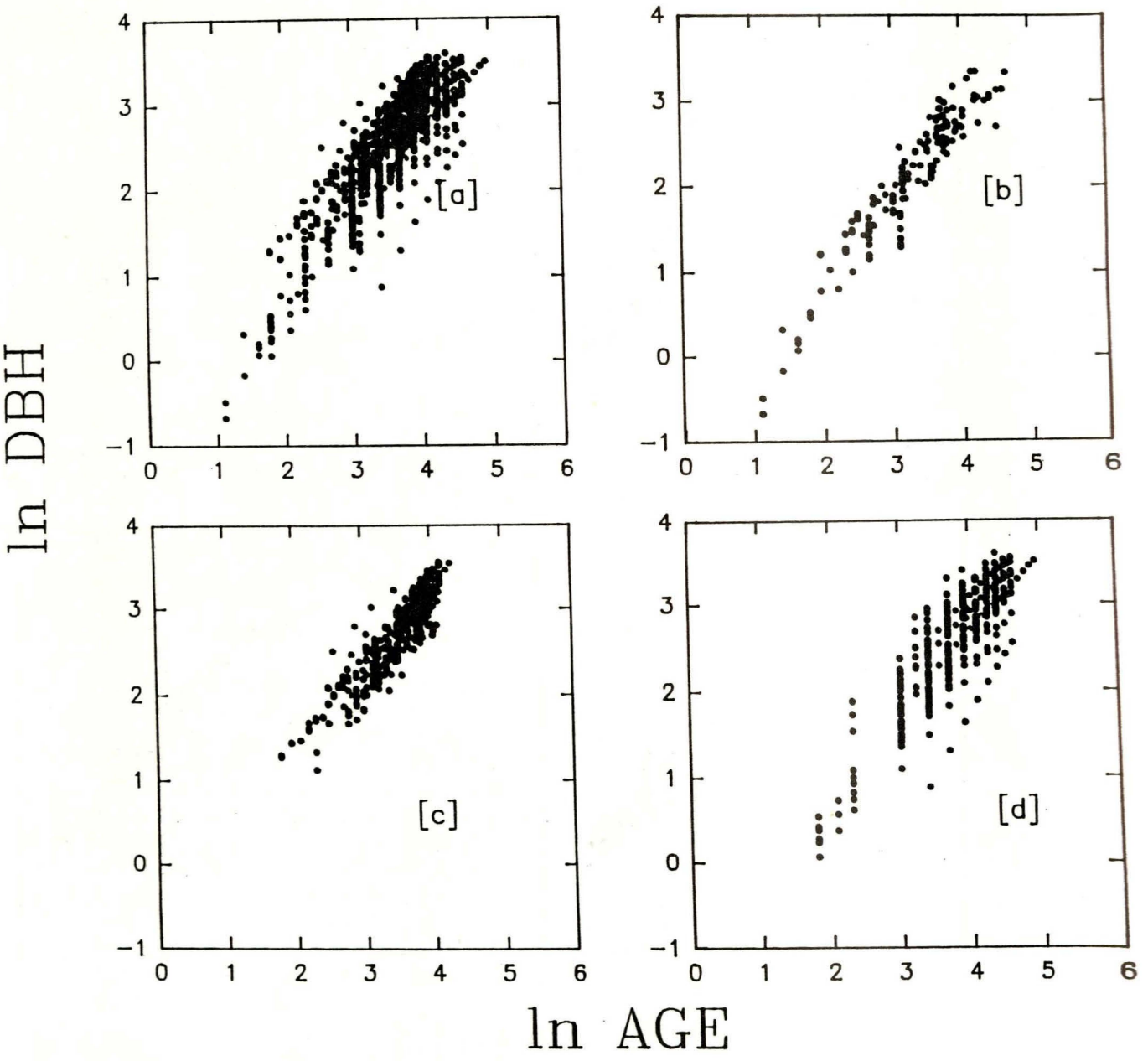

Figure 2.—*The relation of mean stand d.b.h. to stand age (double-logarithmic scale) for (a) the entire data set, (b) the yield set, (c) the dynamic set, and (d) the tabular set.*

Yield

The self-thinning relationship tailed off for stands smaller than just a few cm d.b.h. (fig. 1) as we noticed earlier (Perala *et al.*, in review). Aspen quickly attains horizontal canopy closure and can be self-thinning in the second year (Perala 1984). Early leaf area deficiency seems to be caused by immature canopy structure (Dean and Long 1992). Crown length in self-thinning stands is limited by tree height until a light extinction threshold is reached where lower branches begin to die (Beekhuis 1965). Thereafter, crown length, foliar area, and, by implication, k_2 should remain at some asymptotic maximum value. Moreover, crown shape changes with age (Zeide 1991). For example, Verwijst (1989) found the self-thinning power, -1.37, for *Betula*

pubescens Ehrh. deviated significantly from -1.5 because crown depth diminished as trees grew taller. To maintain constant leaf area during self-thinning, the crowns expanded radially at the expense of packing the space occupied. Crown length data were unavailable to us, but the effect can be estimated from tree height, which is proportional to D^0.8 (Curtis 1970). Of course, tree height is also related to stand age, but the high collinearity between d.b.h. and age (fig. 2) would lead to ambiguous hypothesis testing of associated Student t-values.

In addition to mean d.b.h., stocking was related to climate variables, but better related to mean July air temperature than to precipitation as we found in the truncated data set (Perala *et al.*, in review). The best-fit nonlinear model was

[8] $N = a*(1-c\text{^}D)*d\text{^}J*D\text{^}-b*e_i$

where

N,D = stand variables already described
J = mean July temperature, 17 C maximum
a,c,d = estimated parameters, components of k_2
-b = self-thinning parameter
e_i = error about estimate, geometric mean=1

That is, the self-thinning relationship [8] has a constant power (-b), but the rate parameter (k_2) increases as crown length increases (a function of d.b.h.) and diminishes with temperature.

The fundamental component of model [8],

[9] $N = a*D\text{^}-b$

expresses the self-thinning relationship and trajectories I and II of McFadden and Oliver (1988). Introducing the asymptotic effect of crown length, (1-c^D), and temperature raises the model to trajectory III.

Mean d.b.h. was related to age, site index, and July temperature,

[10] $D = f*A\text{^}g*j\text{^}J*q\text{^}S*e_i$

where

D,A,J,S = variables already described
f,j,q = estimated rate components
g = growth power parameter
e_i = deviation from estimate, geometric mean=1

Similar to [8], the growth relationship [10] has a constant power (g), but the rate paramater increases with site index and with mean July temperature.

Exploratory fitting of the tabular data set confirmed models [8] and [10] were appropriate choices; no better models were discovered.

Dynamics: fully stocked stands

The self-thinning relationship is static and therefore is useful only to describe the standing crop of fully stocked stands. To function as a survival model, a dynamic element is needed. Tait (1988) and Tait *et al.* (1988) used the relationship in dynamic form with good results for fully stocked *P. menziesii* and *P. contorta*. Model [8] provides the basis to develop such a model for fully stocked stands. If we linearize [8] by transforming to the logarithmic mode, and differentiate instantaneous logarithmic relative survival,

$d(\ln N)$, *i.e.* $\ln(N_2/N_1)$

with respect to log relative d.b.h. growth (ignoring (1-c^D) for the moment),

$d(\ln D)$, *i.e.* $\ln(D_2/D_1)$

we obtain the partial derivative

[11] $\ln(N_2/N_1)/\ln(D_2/D_1)=-b$

where

lnN = log number of trees per hectare present at log d.b.h. D
subscript_2 = future value
subscript_1 = starting value
-b = self-thinning power

We consider that the self-thinning power has two components,

$b = b'+w$

where

b' = competition component
w = pathogenic component

In reality, other components contribute to the self-thinning power, including b'*w and episodic events, but these are far beyond the scope of this analysis.

The reciprocal differential, log relative d.b.h. growth with respect to log relative survival,

[12] $\ln(D_2/D_1)/\ln(N_2/N_1)=1/-b$

is also legitimate. Although simultaneous solution of [11] and [12] is possible, dual application to a growth prediction system is difficult. Rather, we reasoned that because mortality in self-thinning stands is growth-driven, and that growth is time-driven, instantaneous log relative d.b.h. growth,

$d(\ln D)$, *i.e.* $\ln(D_2/D_1)$

should be specified with respect to log relative elapsed time,

$d(\ln A)$, *i.e.* $\ln(A_2/A_1)$

to give

[13] $\ln(D_2/D_1)/\ln(A_2/A_1)=g$

where

lnD=log quadratic mean d.b.h. at log age A
g=growth power

Integrating [11] back to the nonlinear mode, including the previously ignored (1-c^D), gives the proportional equation for survival,

[14] $N_2=N_1*(D_2/D_1)^{-b*(1-c^D_2)/(1-c^D_1)}*e_i$

based on the self-thinning relationship. Likewise, integrating [13] gives the proportional equation for radial growth,

[15] $D_2=D_1*(A_2/A_1)^{g}*e_i$

based on the d.b.h.-age relationship.

The observed future value is the starting value for each successive iteration in our analysis. In [14], if $D_2=D_1$, then $N_2=N_1$; in [15], if $A_2=A_1$, then $D_2=D_1$. These are desired attributes of dynamic stand equations (Clutter *et al.* 1983).

Dynamics: understocked stands

The self-thinning relationship needs an asymptotic approach of understocked stands to the maximum size/density constraint (Hara 1984, Smith and Hann 1984, Lloyd and Harms 1986, Harrison and Daniels 1988, Smith and Brand 1988). Stocking is defined as "a more or less subjective indication of the number of trees as compared to the desirable number for best results" (Ford-Robertson 1971). Here we express relative stocking (RS) using given stand density compared to the species boundary line (Clutter *et al.* 1983), expressed as a decimal.

Models [14] and [15] are deficient for understocked stands, and the power parameters must be adjusted accordingly. Consider the conceptual, simplistic growth and survival trajectory of a sparse stand depicted logarithmically in figure 3. At age A_1, RS is much less than 1.0, competition for site resources is lacking, radial growth is maximum at g+p, where

p = residual growth potential,

and only background mortality (w) is at work. At A_2, RS is still sufficiently <1.0 that -b=-w; however, radial growth will have slowed because it

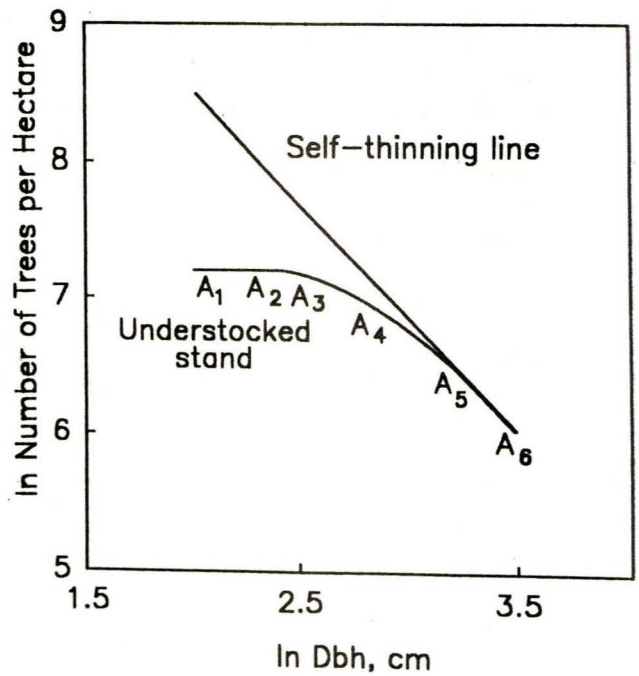

Figure 3.—*Conceptual survival trajectory for an understocked stand inferred from fig. 1 (c).*

has surpassed the threshold of resource limit. From A_3 to A_4, -b asymptotically departs from -w and increases exponentially while radial growth slows further. From A_4 to A_5, mortality asymptotically approaches that given by the self-thinning line (-(b'+w)) as RS approaches 1.0. At RS=1.0, from A_5 to A_6 and beyond, stand dynamics adhere to self-thinning and d.b.h.-age trajectories. Thus, from sparse to dense stands, the doubly asymptotic values of the self-thinning power would range from 0 to -b, and values of the growth power would range from g+p to g.

Clearly, some factor (call it F) must be introduced to allow this flexibility:

[16] $N_2 = N_1*(D_2/D_1)^(-w-b'*F_b)*(1-c^D_2)/(1-c^D_1)*e_i$ and

[17] $D_2 = D_1*(A_2/A_1)^(g+p*F_p)*e_i$

where

$0<=F_b<=1$, $0<=F_p<=1$

From figure 4, and with D_2 given, we infer that F_b depends on potential RS,

Figure 4

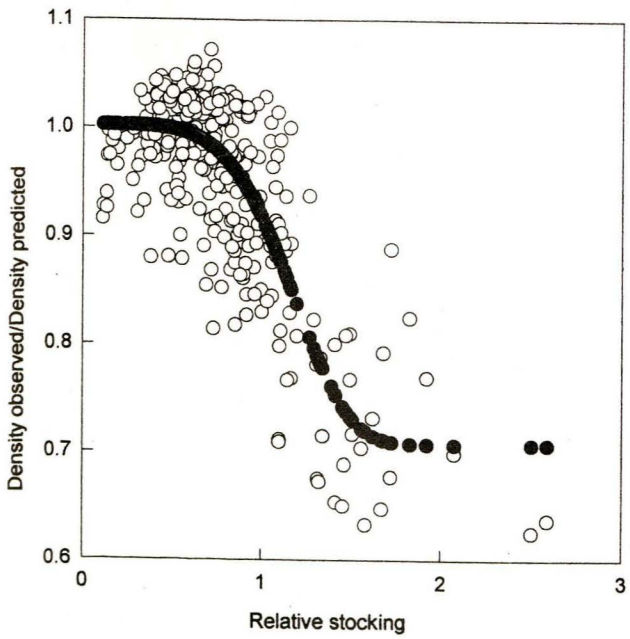

Figure 4.—*Residuals after fitting dynamic data set to model [14] in relation to relative stocking estimated from model [18]. The fitted trend is the Weibull function (eq. [20]) solved in eq. [16].*

Figure 5

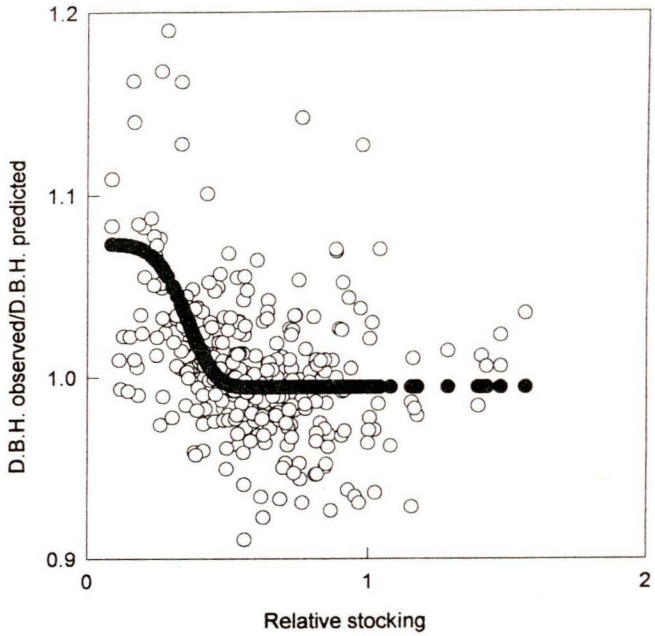

Figure 5.—*Residuals after fitting dynamic data set to model [15] in relation to relative stocking estimated from model [19]. The fitted trend is the modified Weibull function (eq. [21]) solved in eq. [17].*

[18] $RS_2 = N_1/[a*(1-c^D_2)*d^J*D_2^-b]$

Because D_2 is the dependent variable in [17], F_p must be estimated from initial RS,

[19] $RS_1 = N_1/[a*(1-c^D_1)*d^J*D_1^-b]$

Both doubly asymptotic relationships of F to RS (Figs. 4 and 5) can be easily modeled with the Weibull function (Fisher and Tippett 1928, Weibull 1939). A common form based on Yang *et al.* (1978),

[20] $F_b = 1-exp{-[(RS_2/r)^s]}$

where

r = rate parameter
s = shape parameter

is proper for [16]. A modified form,

[21] $F_p = exp{-[(RS_1/r)^s]}$

can model [17]. The Weibull function, noted for its rich expression of curve shapes, is especially

adept at fitting the doubly asymptotic nature of biological processes as well as probability distributions for which it was first developed (Yang *et al.* 1978).

Eq. [16] tests whether RS alters trajectory III of McFadden and Oliver (1988). Eq. [17] tests the effect of RS on radial growth.

Analysis

The yield and dynamic data sets were merged, and a two-step analysis provided compatible yield and dynamic equations that have good fit statistics with minimal bias among data sets. First, logarithmic transformations of stocking models [8] and [16] were fit simultaneously (by nonlinear regression weighted by the inverse of whole-set variance, Wilkinson 1988) to give an average solution of parameters in common. Dummy variables (0,1) were used to control model assignment to data set (Weisberg 1985). Then d.b.h. models [10] and [17] were fit as above except that only the yield set needed logarithmic transformation, and RS_1 (Eq. [19]) was calculated using parameter values solved for [8] and [16].

We also ran weighted nonlinear analyses without logarithmically transforming these models, with little change in outcome. Apparently, logarithmic models adequately stabilized the distribution of e_i.

Verification and Validation

Model behavior was evaluated by studying trends and patterns in bias and accuracy (Burk 1986),

[22] bias percent={100*[geomean(Y_p/Y)-1]}

[23] accuracy percent={100*[geomean(Y_p/Y)-1]}; (Y_p/Y) inverse when <1

where

Y_p = predicted arithmetic value
Y = observed arithmetic value

The yield and tabular data sets were used to evaluate patterns of fit for equations [8] and [10] by study and provenance summary. The dynamic set was used similarly for [16] and [17]. Only the results from the tabular set constitute independent validation.

RESULTS AND DISCUSSION

Stocking and Yield

Aspen yield is a self-thinning relationship in general (fig. 1(b), (d)) and in particular according to trajectory III (tables 2 and 3, eq. [8]). The b parameter, -1.66, lies closer to the parameter value -1.56 for *Alnus rubra*, a similar light-demanding pioneer species, than it does to the -1.92 for *Pseudotsuga menziesii* (Puettmann *et al.* 1993). It is significantly ($p<0.05$) smaller than both the theoretical -1.85 (eq. [5]) and the -1.96 we found with the much smaller data subset (Perala *et al.*, in review), but not significantly larger ($p>0.10$) than Reineke's -1.6.

Why the rather large discrepancy between the b-values of this and our other analysis? Several factors can contribute. First, another term (1-c^D) was introduced to the model. However, the self-thinning relationship seems little confounded with this term that estimates 96 percent of leaf area is acquired by 9.0 cm d.b.h., the lower limit used in our other analysis (Perala *et al.*, in review). Thus, the bulk (about three-fourths) of the data is little influenced by the term. Furthermore, our predictions of leaf area attainment take on some realism when compared to two lines of evidence from the literature. Ruark and Bockheim (1987) studied aspen leaf area over a chronosequence of 8 to 63 years on a single soil series. Their leaf areas agreed closely with our estimates from about 6 cm d.b.h., stabilizing at about 14 cm:

Age	D.b.h.	Leaf area attained	
		Ruark and Bockheim	This study
(yr)	(cm)	(percent)	(percent)
8	3.6	59	71
14	5.5	70	85
18	6.1	85	88
22	9.0	not studied	96
32	14.1	100	99
63	19.2	100	100

Another study by Verry (1987) bears indirectly on this question. Streamflow was greatly enhanced during the first several years after a mature aspen-dominated watershed was clearcut. Flow

Table 2.— *Equation parameter values and statistics*[a]

Parameter[b]	Equation	Value	t-value	Probability
a	[8]	4.049×10^{6}	25.21	0.0000
w	[8],[16]	2.811×10^{-1}	4.61	0.0000
b'	"	1.376	35.48	0.0000
c	"	7.022×10^{-1}	6.72	0.0000
d	"	8.213×10^{-1}	6.15	0.0000
r	[16]	1.215	24.47	0.0000
s	"	4.950	7.58	0.0000
f	[10]	4.807×10^{-2}	10.51	0.0000
j	"	1.071	3.88	0.0001
q	"	1.036	7.88	0.0000
g	[10],[17]	1.009	82.62	0.0000
p	[17]	2.509×10^{-1}	7.54	0.0000
r	"	3.806×10^{-1}	21.58	0.0000
s	"	4.751	3.95	0.0000

[a]Calculated from serial correlation coefficient of residuals (0.315 for [16], 0.104 for [17]) according to Stewart-Oaten and Murdoch (1986).

[b]Parameters a and f adjusted for log bias according to Baskerville (1972).

Table 3.—*Equation fit statistics*[a]

Statistic	Equation			
	[8]	[10]	[16]	[17]
S_{yx}[b]	2259	1.94	81.4	0.493
percent[b]	26.3	19.6	5.49	3.07
adj. R^2	0.961	0.905	0.994	0.995
n	152	154	328	333

[a]Determined by data set from residuals generated by the combined analyses.

[b]At mean Y, calculated according to Baskerville (1972).

subsided to near, but not at, preharvest levels by 15 years as the aspen stand developed into the sapling stage. The return of flow toward the preharvest level was related to greater evapotranspiration and rainfall interception by increasing leaf area. Increased water storage in decomposing logging debris also aided the recovery so that inferred leaf area is exaggerated. This and the Ruark and Bockheim study provide estimates that bracket our predictions of leaf area attainment. A more robust validation awaits additional measurements relating to leaf area. Specifically, does aspen leaf area culminate when d.b.h. averages 15 cm, as [8] predicts? This is equivalent to the 17- to 18-m mean stand height attained in 30 to 40 years on the better sites (Brown and Gevorkiantz 1934, Gregory and Haack 1965).

A second factor is the dominance of the data by the growth set that introduces another term, the Weibull function. Fitting the function unavoidably affects the value of all other parameters through the least squares process, although the great plasticity of the function suggests such influence to be minimal.

Finally, the nature of the yield data may be inconsistent with the species boundary line. Investigators selecting "normal" or "fully stocked" stands routinely bias their choices by discarding stands with "excessive" mortality; *i.e.*, those growing at or near their dynamic thinning lines (Weller 1990). Stands varying in the slope and intercept of the dynamic thinning line and in location relative to the line, and investigator bias proportional to size could easily produce trend data disproportional to the species boundary line. If correct, our analyses show that the species boundary line has a lesser power than is suggested from the trend of normal data.

Despite all this, the utility of the self-thinning relationship is clear. D^-b alone in [8] accounts for 93 percent of the variation in stand density compared to the 96 percent accounted overall (table 3).

Mean d.b.h. of fully stocked stands plotted over age produces a strong and apparently linear relationship (O'Connor 1935, Schlaegel 1971, Bella 1972). We found the relationship [10] linear on logarithmic scales as well (fig. 2), with a power parameter (table 2) not significantly greater than 1.000 ($p>0.40$), meaning virtual linearity.

Age accounted for 85 percent of the total variability in diameter, site index another 4 percent, and mean July temperature another 1 percent. The parameters for these variables indicate for each doubling of age, diameter doubles; for each degree warmer up to 17 C, diameter increases by 7 percent; and for each 3 m improvement in site index, diameter increases by 11 percent. It is well known that as site index increases, d.b.h. invariably increases, other factors being equal (see any yield table).

Stand Dynamics

The survival and growth models ([16] and [17], tables 2 and 3) fit well the wide range of data sources. The S-shaped Weibull function (eq. [20]) was especially critical to fitting the survival model, improving $S_{y.x}$ by 75 percent over eq. [14].

The modified function (eq. [21]) improved $S_{y.x}$ for radial growth by a more modest 15 percent over eq. [15]. This function acting on the parameter p produces the near-linear relation of mean stand diameter over age noticed by Schlaegel (1971) and Bella (1972) when F=0 in self-thinning stands. In contrast, the value of p (table 2) indicates strong nonlinearity (g+p=1.26) in open-grown stands when F=1.

The rate and shape parameters indicate the Weibull function is sharply asymptotic for both growth and survival. These functions confirm that both radial growth and survival were less in dense stands. Neither site nor July temperature is a growth factor here (except that temperature helps determine relative stocking) because each is already integrated into diameter at a given age (*e.g.*, Buckman 1962).

Climatic Relations

The fit of all equations was improved significantly by incorporating the climatic variable, mean July air temperature, to compute stocking (table 2). The coefficient (d) indicates that for each 1 C increase in temperature up to 17 C, stockability diminishes by 18 percent. Aspen longevity is well known to depend in part on a cool climate

(Shields and Bockheim 1981, DeByle and Winokur 1985, Perala 1991). Water deficits associated with warmer temperatures (Thornthwaite and Mather 1955) seem to be the limiting factor (Fralish 1972), probably by limiting leaf area (*e.g.*, Gholz *et al.* 1976, Grier and Running 1977). A favorable water balance allows more foliar transpiring surface that must be supported by greater sapwood area, therefore greater stockability. Because precipitation and air temperature are correlated, it is difficult to partition effects, which is probably why this analysis found temperature rather than precipitation (Perala *et al.* in review) the stronger climatic variable. Neither alone is satisfactory because they operate at odds with each other in the water balance and they operate in concert in tree physiology.

DeBell *et al.* (1989) reported that *Pinus taeda* L. plantations in Hawaii had much greater stockability than they did in the southeastern U.S. Stockability differences were associated with differences in tree size-class structure, canopy depth, and leaf area index that developed under the influence of the contrasting local climates (Harms *et al.* 1994). The prime southeastern site, near Union, South Carolina, is much warmer and somewhat wetter (25.6 C mean July temperature and 1,247 mm annual precipitation) than the Maui, Hawaii, site (15.6 C and 1,143 mm). Canopies in Hawaii were 4 m to 7 m deeper than in South Carolina, and leaf area index was five times greater. The favorable driving influences of the Hawaiian climate were thought to be long growing season, high solar radiation, high sun angle, and favorable temperatures. Given that aspen regenerates greater densities in warm environments (Schier *et al.* 1985) where its life is shorter, a significant temperature term is not surprising.

Diameter, in contrast, increases by 7 percent per degree warming up to 17 C. Warm growing seasons should affect apical and cambial activity proportionately (Fraser 1962, Jones and Schier 1985) so that most of the temperature effect would be inherent in site index. Given that stockability diminishes by 18 percent per 1 C, the inverse relationship (*c.f.* [4] and [5]) implies that d.b.h. should increase 22 percent (1/(1-.18)) per 1 C rather than 7 percent. This 15-point deficiency is added evidence that radial growth is more sensitive to stress than is survival. Again, the stress is probably more related to water deficiency than to temperature *per se* (Jones and Schier 1985).

Validation

Pattern analysis revealed that the dynamic models performed well with little bias and good accuracy among data sources, both singly and aggregated by provenance (tables 4, 5, 6). Predicted basal area growth (from [17], and [16] estimated from the output of [17]) fit observed basal area growth about as well (R^2=.52, sd=44 percent of mean growth) as in the model used by Schlaegel (1971) on a locally restricted subset of these data (R^2=.45, sd=37 percent).

On the other hand, much local and regional bias remains in the yield data set, and especially in the tabular set (tables 4, 5, 6). Although the temperature term reduced prediction bias, the stockability of aspen in Newfoundland was still greatly underestimated (table 5). Much like the Hawaii site mentioned earlier (Harms *et al.* 1994), Newfoundland has cool summers (July temperatures barely average 16 C) and as much as 1,200 mm precipitation annually, half again as much as any of our other data sources (Page 1972, Pearse *et al.* 1985). Such a climate provides a most favorable water balance for aspen growth (Sucoff 1982). A water availability term (*e.g.*, Grier and Running 1977) in addition to, or in place of, the temperature term might aid stocking predictability.

When stocking bias is examined for trends across d.b.h. classes (table 5), and d.b.h. bias is examined over age classes (table 6), five different patterns among provenances emerge:

1. little bias trend for either stocking or d.b.h. (Alaska, Saskatchewan, Minnesota);
2. stocking bias negative power, d.b.h. bias positive power (Manitoba, Ontario, Newfoundland, *P. grandidentata*);
3. stocking bias negative power, no d.b.h. trend (Alberta);
4. stocking bias convex, d.b.h. bias concave (Rocky Mountains, Michigan);
5. stocking bias convex, d.b.h. bias positive power (*P. tremula*).

Table 4.—*Pattern analyses of equations [8], [10], [16], and [17] by provenance and author*

Author	Equations [10], [17] (diameter)					Equations [8], [16] (trees)		
	Data set[a]	Cases	Mean	Bias	Accuracy	Mean	Bias	Accuracy
			mm	*- - - Percent- - -*		*n/ha*	*- - - Percent- - -*	
Alaska								
Gregory and Haack 1965	T	37	107	36	36	6,377	9	9
Saskatchewan								
Bella 1975	Y	6	11	26	26	47,060	10	12
Bella and DeFranceschi 1980	T	15	53	24	24	16,630	-12	18
Kirby *et al.* 1957	T	27	149	20	20	2,619	20	20
Steneker 1969	D	21	20	3	3	408	-3	4
Steneker 1969	Y	10	57	-3	4	7,246	9	19
All	Y	16	40	8	12	22,170	9	16
All	T	42	115	22	22	7,624	9	19
Manitoba								
Pike 1953	D	3	60	-1	6	1,523	12	12
Pike 1953	Y	4	98	22	22	3,772	7	7
Steneker 1974	D	51	30	0	5	478	2	7
Steneker 1974	Y	29	80	-2	11	6,339	-5	15
All	D	54	31	0	5	536	2	7
All	Y	33	82	1	12	6,028	-4	14
Alberta								
Bella 1975	Y	3	12	19	19	48,110	3	5
Bella and DeFranceschi 1980	T	18	45	28	28	19,930	4	23
Rocky Mountains								
Baker 1925	T	5	287	22	22	642	3	3
Bartos and Lester 1984	Y	3	162	-16	16	2,900	-41	41
Crouch 1981	Y	1	200	-13	13	1,312	-4	4
Jones and Trujillo 1975	Y	6	44	18	18	19,690	-23	32
Kemperman and Barnes 1976	Y	2	254	14	14	1,327	-62	62
Schier 1975	Y	5	188	6	10	1,135	23	23
Schier and Smith 1979	Y	1	212	2	2	907	4	4
Walters *et al.* 1982	Y	3	250	-27	27	927	-18	18
All	Y	21	160	1	16	6,674	-15	29
Minnesota								
Brown and Gevorkiantz 1934	T	27	170	4	9	2,137	7	8
Hubbard 1972	D	6	27	5	9	852	-5	7
Hubbard 1972	Y	4	64	-8	9	5,651	5	11
Noreen 1968	D	5	30	1	7	441	-2	5
Noreen 1968	Y	9	36	5	22	17,420	3	12
Perala 1974	D	7	25	-11	11	4,806	-7	8
Perala 1978	D	48	26	-2	3	128	3	5
Perala 1978	Y	7	114	-5	9	3,533	3	5
Perala 1979	Y	2	21	2	4	29,450	-29	34

(Table 4 continued on next page)

(Table 4 continued)

Author	Equations [10], [17] (diameter)					Equations [8], [16] (trees)		
	Data set[a]	Cases	Mean	Bias	Accuracy	Mean	Bias	Accuracy
			mm	*- - -Percent- - -*		*n/ha*	*- - -Percent- - -*	
Perala 1984	Y	2	50	-10	10	9,345	-21	21
Perala data filed	D	19	19	0	3	394	2	5
Perala data filed	Y	6	88	11	11	3,929	15	15
Perala and Alban 1982	Y	2	209	-23	23	1,022	-6	11
Perala and Laidly 1989	D	24	12	1	3	20	1	2
Schlaegel 1971, 1972	D	60	27	0	2	89	7	7
Schlaegel 1975	Y	1	182	-20	20	1,334	-17	17
Schlaegel and Ringold 1971	D	8	26	0	2	31	5	5
All	D	177	24	0	3	343	3	6
All	Y	33	80	-1	14	9,354	1	13
				Michigan				
Barnes 1969	Y	3	86	6	7	2,723	45	45
Day 1958	D	3	20	6	6	82	3	5
Day 1958	Y	7	56	7	8	8,566	-6	17
Graham *et al.* 1963	T	16	171	-26	26	961	51	51
All	Y	10	65	7	8	6,813	9	26
				Ontario				
Plonski 1960	T	51	190	1	10	1,337	18	18
				Newfoundland				
Page 1972	T	8	137	15	15	3,614	-29	34
				Europe (*P. tremula* and hybrid)				
Elfving 1986	D	4	58	-2	11	55	-6	7
Haugberg 1958	D	69	15	1	2	<1	-1	1
Haugberg 1958	Y	34	144	-2	15	1,862	19	27
Vincent *et al.* 1950	T	50	162	0	20	2,227	10	20
Vuokila 1977	D	11	22	1	3	34	-3	3
Vuokila 1977	Y	2	40	21	21	12,950	16	24
All	D	84	18	1	2	7	-2	2
All	Y	36	139	-1	15	2,478	19	27
TOTAL *P. tremuloides, tremula*	D	339	23	0	4		1	5
TOTAL *P. tremuloides, tremula*	Y	152	99	2	14		3	20
				P. grandidentata				
Graham *et al.* 1963	T	19	184	-28	28	936	24	27
Koerper and Richardson 1980	Y	3	166	21	21	1,474	-1	18

[a] T = tables, Y = yield, D = dynamic.

Table 5.—*Pattern analyses of equations [8] and [16] by quadratic mean d.b.h. class, data set, and provenance*

Provenance	Cases	Quadratic mean d.b.h. class, cm							Mean
		<5	5	10	15	20	25	>25	
					Bias, percent				
Dynamic data set (eq. [16])									
Saskatchewan	21		-9	-2	-1				-3
Manitoba	54		2	3	2	1	-2		2
Minnesota	177		-3	2	6	5	6	5	3
Michigan	3			3					3
P. tremula	84		-7	-4	-2	-1	-1	-2	-2
MEAN			-3	1	2	2	4	4	1
CASES			39	83	80	71	45	21	339
Yield data set (eq. [8])									
Saskatchewan	16	10	13	-7					9
Manitoba	33		4	-5	-20				-4
Alberta	3	3							3
Rocky Mountains	21		-23		-17	-2	-11	-36	-15
Minnesota	33	-16	7	-2	4	-11	5		1
Michigan	10		-13	42					9
P. tremula	36		7	18	17	44		6	19
MEAN		0	2	7	5	10	-7	-22	3
CASES		13	53	37	29	13	4	3	152
Tabular data set (eq. [8])									
Alaska	37	8	9	9	8	8			9
Saskatchewan	42	10	8	-3	15	20	14	12	9
Alberta	18	29	-13	-26					4
Rocky Mountains	5						4	3	3
Minnesota	27		17	9	6	6	3	2	7
Michigan	16			60	56	46	37	32	51
Ontario	51		60	31	17	15	9	9	18
Newfoundland	8		10	-16	-41	-56			-29
P. tremula	50		11	21	14	7	0	-5	10
MEAN		22	9	15	14	12	8	4	12
CASES		13	44	61	45	42	27	22	254
***P. grandidentata* data set (eq. [8])**									
Michigan	22			56	24	9	15		20

Table 6.—*Pattern analyses of equations [10] and [17] by age class, data set, and provenance*

Provenance	Cases	Age class, years							Mean
		<10	10	20	30	40	50	>50	
		- - - - - - - - - - - - Bias, percent - - - - - - - - - - - -							
					Dynamic data set (eq. [17])				
Saskatchewan	21			3	2				3
Manitoba	54			-4	-1	2		-1	0
Minnesota	177		0	-2	0	0	1	0	0
Michigan	3			6					6
P. tremula	84		-17	-1	5	1	0	0	1
MEAN			-1	-1	0	1	1	0	0
CASES			26	75	56	77	70	35	339
					Yield data set (eq. [10])				
Saskatchewan	16	44	-1	1	1				8
Manitoba	33		-8	1	-3	11		16	1
Alberta	3	19							19
Rocky Mountains	21			18			-23	-4	1
Minnesota	33	24	-3	4	0	-12	-27		-1
Michigan	10		13	5		7			7
P. tremula	36		22	-11	-2	-3	9	-6	-1
MEAN		29	-2	5	-1	0	-1	-3	1
CASES		8	32	36	12	39	7	18	152
					Tabular data set (eq. [10])				
Alaska	37			22	40	37	35	38	36
Saskatchewan	42		18	18	29	30	21	18	22
Alberta	18		29	24	27	32			28
Rocky Mountains	5							22	22
Minnesota	27			1	7	11	9	0	4
Michigan	16			-21	-26	-34	-24		-26
Ontario	51			-16	-11	-6	-3	8	1
Newfoundland	8			8	14	11	9	20	15
P. tremula	50		-54	-19	-11	-6	1	17	0
MEAN			12	0	9	8	7	17	11
CASES			18	34	32	38	26	106	254
					***P. grandidentata* data set (eq. [10])**				
Michigan	22			-50	-41	-32	-5	3	-21

Such variability indicates additional environmental or genetic control of both the rate and power parameters of the self-thinning and growth-age relationships beyond our ability to explain with the given data base. Developing local equations or accepting variability as noise on a global scale are the only alternatives until we can develop ecophysiological models (Rauscher *et al.* 1990) that better reflect the growing environment. Although local genetic variability can be overwhelming (Jones and DeByle 1985), it is not necessarily a deterrent. For example, three of the studies in this analysis are on the same soil series, Warba fine sandy loam (Perala and Alban 1982), but as much as 8 km apart (Schlaegel 1971; Perala 1974, 1978). The overall accuracy was 4 percent for diameter estimation and 5 percent for stockability, despite the many clones included.

Stockability of largetooth aspen was significantly greater than quaking aspen in the same locale (Graham *et al.* 1963 in table 5). The Eurasian aspens did not clearly differ from quaking aspen.

CONCLUSIONS

The asymptotic diameter-density limiting relationship provided a powerful framework to evaluate the variability of growth and yield of aspen. Certainly, aspen conforms to self-thinning relationships, but the rate parameter and perhaps even the power parameter appear to be driven in part by the local growing environment. Genetic variability at the clone level, beyond that expressed as measured site index, likely affects these coefficients as well. Other sources of variation might include study technique, plot size, and investigator bias. The resolution of these generic equations improves with scale. Better local estimates can be gained by refitting the models to local data.

Relating aspen growth more accurately to its environments, particularly water stress or water use (*e.g.*, Wickramasinghe 1988), requires an even broader, balanced, and intensive data base, both from the field and from provenance studies. Packing relationships probably could be improved with estimates of soil water capacity that mediate frequency and duration of water stress (Thornthwaite and Mather 1955). To better quantify these effects, periodic growth data are particularly needed for the extreme climates of the Rockies, Alaska, Newfoundland, the Maritimes, and the warmest extremities of the aspen range.

ACKNOWLEDGMENTS

We thank I. Bella, R. McRoberts, and T. Mowrer for their helpful reviews of an earlier draft. We dedicate this paper to Bryce E. Schlaegel, who enlightened our understanding of aspen productivity. He died much too young in Atlanta, Georgia, in March 1990.

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1995. **Stockability, growth, and yield of the circumboreal aspens (*Populus tremuloides* Michx., *P. tremula* L.)**. Res. Pap. NC-321. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 24 p.

Examines the d.b.h.-age and stockability relationships in aspen stands of varying ages and densities. Accounts for the curvilinear trend in the self-thinning relationship in young aspen stands.

KEY WORDS: survival, self-thinning, size-density, limiting relationship.

Our job at the North Central Forest Experiment Station is discovering and creating new knowledge and technology in the field of natural resources and conveying this information to the people who can use it. As a new generation of forests emerges in our region, managers are confronted with two unique challenges: (1) Dealing with the great diversity in composition, quality, and ownership of the forests, and (2) Reconciling the conflicting demands of the people who use them. Helping the forest manager meet these challenges while protecting the environment is what research at North Central is all about.

☆U.S. GOVERNMENT PRINTING OFFICE: 1995 - 656-926